

CHOICE BETWEEN REPLETING/DEPLETING PATCHES:
A CONCURRENT-SCHEDULE PROCEDURE

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Six pigeons responded on two concurrently available keys that defined patches with the following characteristics. Reinforcer stores repleted on a patch as a linear function of time when the bird had last responded to the other patch, or else did not replete. Repletion schedules thus timed only when the bird was absent from the patch. Reinforcer stores on a patch could be depleted and reinforcers obtained, again as a linear function of time, when the bird responded on a key. Depletion schedules thus timed only when the birds were present at a patch. Experiment 1 investigated changing relative depletion rates when repletion rates were constant and equal (Part 1) and changing relative repletion rates when the depletion rates were constant and equal (Part 2). Response- and time-allocation ratios conformed to a generalized matching relation with obtained reinforcer ratios, and there appeared to be no control by the size of the reinforcer stores. In Experiment 2, absolute depletion rates were varied with a pair of unequal repletion rates (Part 3), and absolute repletion rates were varied with a pair of unequal depletion rates (Part 4). Dwell times in the patches were not affected by either variation. Melioration theory predicted the results of Experiment 1 quite closely but erroneously predicted changing dwell times in Experiment 2. Molar maximization theory did not accurately predict the results of either experiment.

Key words: concurrent schedules, patches, repletion, depletion, choice, generalized matching, pecking, pigeons

In the experimental analysis of behavior, a great deal of research has been done on performance in concurrent schedules of reinforcement, and a great deal is known about how various animals distribute their behavior when alternatives differ with respect to food frequency, delay, quality, deprivation, and magnitude, and with respect to the force or type of the required response (e.g., Davison & McCarthy, 1988). The burgeoning interest in animal choice in the wild—*foraging*—has highlighted the question of whether the results of laboratory-based research in the experimental analysis of behavior can be generalized to behavior in the wild. Some (e.g., Baum, 1982) have argued that the matching relation that occurs under concurrent schedules in the laboratory may also characterize choice in the wild. However, the ways in which the natural

environment behaves and responds to animal behavior are much more diverse than the procedures traditionally investigated in the laboratory. Despite these differences, Houston (1986) showed that the distribution of time by wagtails between river-bank territories and meadow patches followed the distribution of rewards obtained in these patches. It may be, therefore, that the matching relation does apply to the foraging of at least some animals in the wild.

There are many differences between the laboratory procedure of concurrent variable-interval (VI) schedules and natural foraging conditions, apart from the obvious difference in setting. First, on concurrent VI schedules, patches replete at a constant rate when the animal is at that patch and at a similar rate when it is absent *up to a limit of a single food item*. (The relatively unusual procedure of linear VI programming [Herrnstein & Vaughan, 1980; Vaughan, 1982] does arrange that more than a single food item can be available on a patch.) Second, patches cannot generally be depleted to a continuous level of zero food items because the schedules continue to time and to set up food deliveries. Third, the repletion rate of a patch is equal to the depletion rate, at least when the subject is in a patch. Thus, the

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procedure cannot differentiate whether choice is controlled by depletion rates (rates of gaining food) or repletion rates (rates at which food becomes available). A simple question might be: Given a choice between two equal depletion rates (rates of discovering food), would an animal spend more time at a patch that contained a greater number of food items before depletion to zero occurred? This seems likely, but an answer to the inverse of this question is more difficult: Given a choice between two equal repletion rates, would an animal show a preference for the higher depletion rate? If it did, of course, it would be likely to drive continually the preferred patch to zero prey availability. A better strategy might be to spend equal time at the two patches, gaining the higher rate of food at the richer patch. It may well be that in one or both of these simple cases, the matching of relative time allocation to relative obtained reinforcers, as found in the laboratory, would not occur.

There is a need, as Shettleworth (1989) has pointed out, for laboratory procedures that mimic better some of the features of the natural environment. Such procedures also need to be rather generally modifiable for investigating a wide range of possible natural-environment features. The present experiment was an investigation of one such procedure. It used the standard laboratory situation modified to simulate at least some of the features of the natural environment. Two patches were arranged. Via repletion schedules, the number of food deliveries stored in each patch increased, on average, linearly with the time that the animal was absent from each patch. A linear increase was used for simplicity; any kind of function could be arranged, from a decreasing function (predation of the patch by other foragers) to a standard population-dynamic increase. Repletion did not occur when the animal was at the patch, although repletion at a lower rate (e.g., due to interference from the forager with reproduction) could be arranged. The stored food items at each patch could be depleted, again at a constant average rate in this experiment, when the animal was in the patch. Again, linear depletion was used for simplicity, although a depletion schedule that provided diminishing returns, either as a function of time spent or on number of prey remaining, would be more natural.

The pigeons were free to change between

patches at all times, and no explicit period of time (travel time) or work requirement was arranged in this experiment.

The experiment was designed as a simple parametric empirical investigation of this procedure. There were two parts to Experiment 1, which investigated the effects of changing relative depletion rates with constant and equal repletion rates (Part 1) and the effects of varying relative repletion rates with constant and equal depletion rates (Part 2). Experiment 2 investigated the effects of varying overall depletion with constant and equal repletion rates (Part 3) and of varying overall repletion rates with constant and equal depletion rates (Part 4). As in matching experiments, the data of interest were relative time and response allocation between the patches. From a more naturalistic viewpoint, the absolute dwell times at the patches and the number of food items not obtained are of interest.

GENERAL METHOD

Subjects

Six homing pigeons, numbered 31 to 36, were maintained at $85\% \pm 15$ g of their free-feeding body weights. They were housed individually and had free access in their home cages to water and grit. These birds had previously been trained on a variety of concurrent schedules with delayed reinforcement (Davison, 1988), and so required no pretraining.

Apparatus

The experimental chamber, which was situated remote from the computer that controlled the experiment, was 330 mm high, 330 mm wide, and 310 mm deep. It was fitted with an exhaust fan that provided ventilation and some masking noise. On one wall of the chamber were three response keys, 20 mm in diameter, 110 mm apart, and 250 mm from the grid floor. Only the outer two keys were used in this experiment. When these keys were transilluminated white, pecks on them exceeding about 0.1 N operated the keys. The food magazine, which was situated beneath the center key 120 mm from the floor, contained wheat. During reinforcer delivery, the key-lights were extinguished (becoming inoperative) and the magazine was raised and illuminated for 3 s. There was no other illumination in the chamber.

Table 1

Sequence of experimental conditions, number of training sessions, and probabilities of reinforcement per second ($p(R/s)$) in each experimental condition.

Condi- tion	Repletion $p(R/s)$		Depletion $p(R/s)$		Initial store		Sessions
	Left	Right	Left	Right	Left	Right	
Experiment 1							
Part 1							
2	.0170	.0170	.0250	.0250	2	2	24
3	.0170	.0170	.0400	.0100	3	1	21
4	.0170	.0170	.0050	.0450	1	3	26
5	.0170	.0170	.0450	.0050	3	1	23
6	.0170	.0170	.0100	.0400	1	3	32
Part 2							
7	.0272	.0068	.0250	.0250	2	2	19
8	.0034	.0306	.0250	.0250	2	2	34
9	.0306	.0034	.0250	.0250	2	2	27
10	.0068	.0272	.0250	.0250	2	2	32
11	.0170	.0170	.0250	.0250	2	2	20
Experiment 2							
Part 3							
12	.0272	.0068	.0250	.0250	2	2	17
13	.0068	.0272	.0200	.0200	2	2	30
14	.0272	.0068	.0175	.0175	2	2	39
15	.0068	.0272	.0150	.0150	2	2	25
16	.0272	.0068	.0125	.0125	2	2	30
17	.0068	.0272	.0100	.0100	2	2	41
18	.0272	.0068	.0075	.0075	2	2	38
Part 4							
19	.0300	.0300	.0100	.0400	1	3	24
20	.0250	.0250	.0400	.0100	3	1	24
21	.0200	.0200	.0100	.0400	1	3	20
22	.0150	.0150	.0400	.0100	3	1	27
23	.0100	.0100	.0100	.0400	1	3	24
24	.0050	.0050	.0400	.0100	3	1	23

Procedure

The daily sessions commenced when the subject was placed in the darkened chamber. Shortly thereafter, the outer keys were illuminated white, and food reinforcers became intermittently available for responses on these keys. The session ended when 40 reinforcers had been delivered or when 45 min had elapsed, whichever event occurred first.

The general procedure was as follows. There were two pairs of VI schedules, all of which arranged events with fixed probabilities per second. One pair of schedules were repletion schedules that added reinforcers to two stores of reinforcers, one associated with each key. There was no maximum on the number of reinforcers that could be stored in this way. At the beginning of each session, four reinforcers were already stored, and the size of these stores

was correlated with the depletion rates on the keys (Table 1). The repletion schedule for each key timed, and could add reinforcers to the store associated with that key, only when the subject was responding on the other key—that is, from the first response on the other key until the first response again emitted on the key whose store had been repleting. Time-allocation measures were defined in the same way.

The second pair of VI schedules were depletion schedules. These provided the subjects with access to the stored reinforcers and operated only when the subject was responding on a key—from the first response on that key to the first response on the other key. Thus, in terms of foraging, each patch repleted only when the subject was not foraging at that patch and could be depleted only when the subject

was at that patch. The food resources at a patch increased, on average, linearly when the subject was absent, and could be decreased, on average, linearly when it was present. Patches could be depleted to zero but not beyond. Both the repletion and depletion timers ran during reinforcer deliveries.

All experimental contingencies were controlled by a PC compatible computer running Med-State Notation®. The data collected were the number of pecks and the time spent responding on the two keys, the number of reinforcers obtained from each key, the number of changeovers between the keys, and the number of reinforcers remaining in the stores associated with each key. Experimental conditions (Table 1) remained in effect until all subjects had met a stability criterion five, not necessarily consecutive, times. The criterion was that the median relative number of responses to one key over five sessions did not differ by more than .05 from the median of the immediately preceding five sessions. Thus, at least 14 sessions were required for stability to be achieved. When all subjects had met this criterion five times, the experimental conditions were changed for all subjects. Typically, once each bird had met this criterion, relative response rate remained stable until conditions were changed.

Condition 1 was a training condition with high repletion and depletion probabilities per second on each patch, and these data are not reported here. Table 1 shows all the conditions of Experiments 1 and 2. In Experiment 1, Part 1 (Conditions 2 to 6), repletion rates were kept constant and equal at .017 per second, and relative depletion rates were varied. In Part 2 (Conditions 7 to 11), depletion rates were kept constant and equal at .025 per second and relative repletion rates were varied. Experiment 2, Part 3 (Conditions 12 to 18) investigated the effects of varying absolute depletion rates (keeping them equal) from .0075 to .025 per second over seven conditions, with the repletion of .0272 and .0068 alternated between the keys across conditions. Part 4 (Conditions 19 to 24) maintained equal repletion probabilities but varied their absolute values from .005 to .03 per second and alternated depletion probabilities per second of .01 and .04 between the keys in successive conditions.

EXPERIMENT 1

In Part 1 (Conditions 2 to 6), the repletion probability was .017 per second for both keys, and the depletion probabilities per second were varied between .005 and .045 to .045 and .005 on the two keys over five experimental conditions (Table 1). In Part 2 (Conditions 7 to 11), the depletion probabilities were .025 per second for both keys, and the repletion probabilities per second were varied between .0034 and .0306 to .0306 and .0034 over five conditions.

RESULTS

Tables of raw data from each subject and condition are in the appendix. The data analyzed here were from the last five sessions of each experimental condition.

In Part 1, the repletion probabilities were .017 per second on each key (1.02 reinforcers added to the store per minute on average), while the depletion probabilities were varied over five experimental conditions from .005 (0.3 reinforcers per minute) and .045 (2.7 per minute) to the reversal of these probabilities. Both response allocation and time allocation were strongly and directly influenced by the depletion rates. Figure 1 shows, for all 6 birds, the relation between the log response- and time-allocation ratios and the log obtained reinforcer ratios. Straight lines were fitted to the data using the least squares procedure. The slopes and intercepts are shown on the graphs, and more details about the fits are shown in Table 2. The slopes varied from 0.28 to 0.80 (responses) and from 0.34 to 0.90 (time) and averaged 0.65 for both measures. Between 82% and 100% of the data variance was accounted for. The response-allocation slopes were greater than the time-allocation slopes for 3 of the 6 subjects, and hence not significantly different. The slopes were reasonably close to, but rather lower than, slopes expected for concurrent VI VI schedules (Baum, 1979; Taylor & Davison, 1983; Wearden & Burgess, 1982).

Dwell, or interchangeover, times for each subject in Part 1 are shown in Figure 2 as a function of the relative frequency, $R_i/(R_i + R_j)$, of reinforcers obtained. As the time-allocation ratio data in Figure 1 suggest, the dwell times on the two keys changed with changing frequencies of obtained reinforcers,

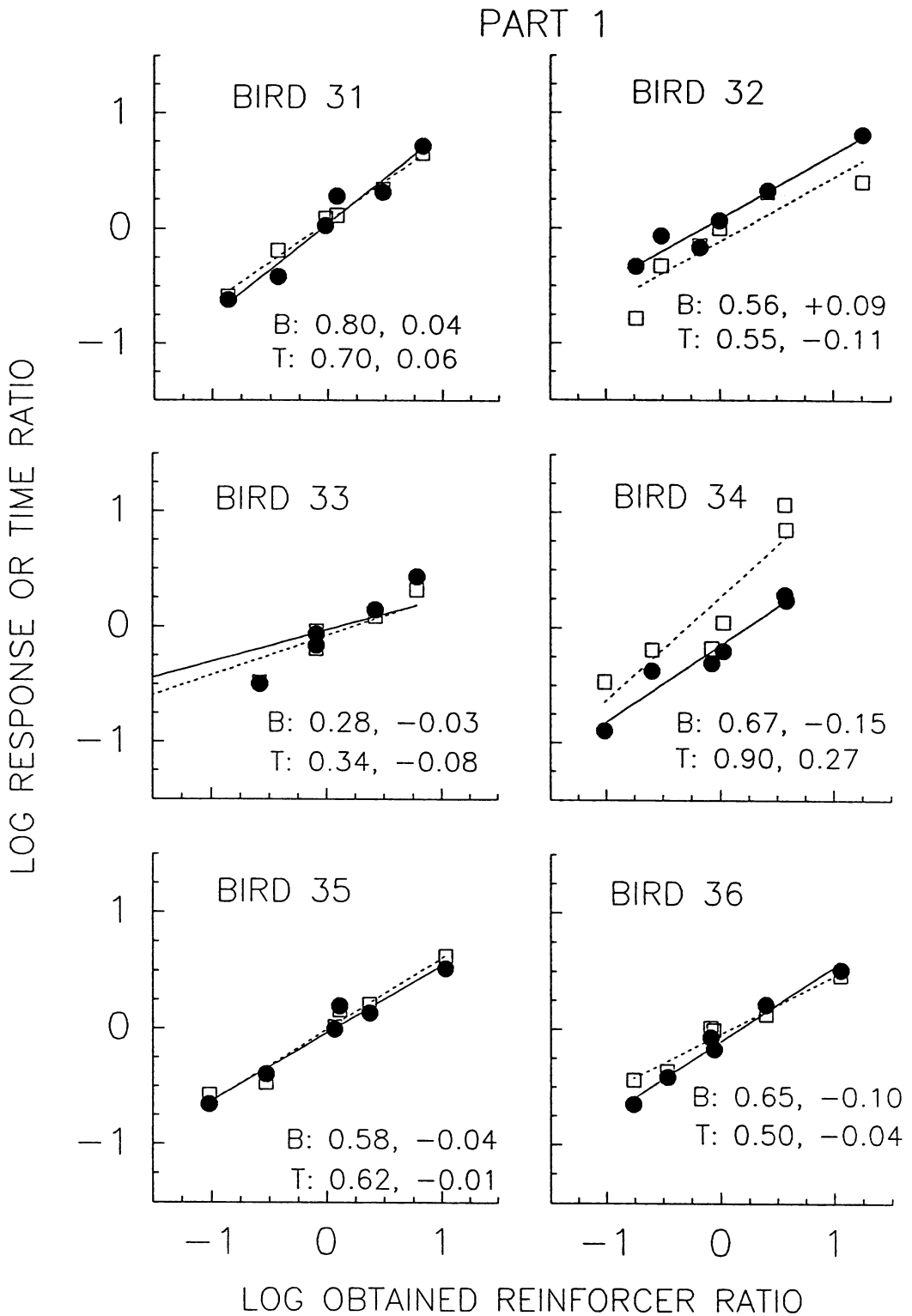


Fig. 1. Experiment 1, Part 1. Log response- and time-allocation ratios (L/R) as a function of log obtained reinforcer ratios for each subject when repletion rates were constant and equal and depletion rates were varied. The straight lines are the lines of best fit by least squares linear regression, and the slope and intercept of these lines for response (B) and time (T) allocation are shown on the graph. One data point for Bird 33 fell off the graph.

Table 2

Results of regression analyses between log response or time ratios and log obtained reinforcer ratios in Experiment 1. *SE* is the standard error of the fit, and *VAC* is the percentage of data variance accounted for.

Bird	Slope (<i>SD</i>)	Intercept	<i>SE</i>	<i>VAC</i>
Part 1: Responses				
31	0.80 (0.09)	0.04	0.12	95
32	0.56 (0.06)	0.09	0.10	95
33	0.28 (0.06)	-0.03	0.22	82
34	0.67 (0.08)	-0.15	0.12	94
35	0.58 (0.06)	-0.04	0.09	96
36	0.65 (0.05)	-0.10	0.07	98
Group	0.65 (0.01)	-0.03	0.02	100
Part 2: Responses				
31	0.76 (0.10)	-0.12	0.08	95
32	0.80 (0.05)	0.12	0.04	99
33	0.83 (0.09)	0.06	0.07	97
34	0.61 (0.06)	-0.05	0.06	97
35	0.78 (0.18)	0.14	0.17	86
36	0.72 (0.06)	0.02	0.05	98
Group	0.77 (0.07)	0.04	0.06	98
Part 1: Time				
31	0.70 (0.04)	0.06	0.05	99
32	0.55 (0.13)	-0.11	0.20	83
33	0.34 (0.04)	-0.08	0.14	94
34	0.90 (0.20)	0.27	0.28	83
35	0.62 (0.06)	-0.01	0.09	97
36	0.50 (0.05)	-0.04	0.08	96
Group	0.65 (0.03)	-0.02	0.04	99
Part 2: Time				
31	0.99 (0.06)	-0.03	0.05	99
32	0.83 (0.20)	-0.17	0.16	85
33	0.92 (0.07)	-0.07	0.06	98
34	0.47 (0.24)	0.04	0.23	57
35	0.84 (0.15)	0.12	0.14	92
36	0.79 (0.19)	-0.18	0.16	85
Group	0.80 (0.05)	-0.05	0.04	99

and equal dwell times were obtained with equal frequencies. However, the dwell times appeared to be considerably longer than those usually produced on concurrent VI VI schedules with similar reinforcer rates (e.g., Tustin & Davison, 1979).

Figure 3 shows log ratios of response and time allocation as a function of the log ratio of obtained reinforcers in Part 2 when depletion rates were constant and equal and relative repletion rates were varied. Straight lines were fitted to these data by the method of least squares, and the slopes and intercepts of the regressions are shown on the figure. More detail about the fits is shown in Table 2. The slopes varied from 0.61 to 0.83 for response measures ($M = 0.77$) and from 0.47 to 0.99

($M = 0.80$) for time measures. There was no statistically significant difference between response and time slopes on a normal-scores test at $p = .05$. Intercepts were usually close to zero and did not deviate from zero in any particular direction. Some of the intercepts were reasonably large (e.g., Birds 31, 32, and 35 for response measures, and Birds 32, 35, and 36 for time measures), but these, too, were in no consistent direction. Figure 4 shows that dwell times in Part 2 as a function of relative reinforcers obtained were very similar to those found in Part 1.

Comparing the results of Parts 1 and 2, on normal-scores tests there were no statistically significant differences between either response- or time-allocation slopes across the two different procedures ($p > .05$). However, comparison of Figures 1 and 3 and 2 and 4 shows a clear difference in the range of relative reinforcer rates obtained, which was much smaller in Part 2. Relative obtained reinforcers, responses emitted, and reinforcers uncollected are shown as a function of relative arranged depletion (Part 1) and repletion (Part 2) rates in Figure 5. The smaller variation in relative obtained reinforcers in Part 2 compared to Part 1 is clear, as is the smaller variation in relative responses emitted. However, the relation between relative responses and relative reinforcers obtained was similar in both parts, as shown in the comparison of Figures 1 and 3.

Also of interest in Figure 5 is the distribution of reinforcers remaining at the end of sessions. In Part 1, as the relative depletion rate on a key increased, relatively fewer reinforcers were left available on that key at the end of the session. The results were quite different for Part 2. Increasing the relative repletion rate on a key increased the relative number of reinforcers remaining on that key at the end of the session. Thus, the subjects did not keep responding on a key while reinforcers remained on that key, even though they could obtain them at the same rate as on the other key. However, relative numbers can be misleading, and Figure 6 shows the absolute numbers of reinforcers obtained and reinforcers remaining after sessions as a function of the relative depletion and repletion rates, averaged across the subjects and the last five sessions. The number of obtained reinforcers followed the relative depletion and repletion rates

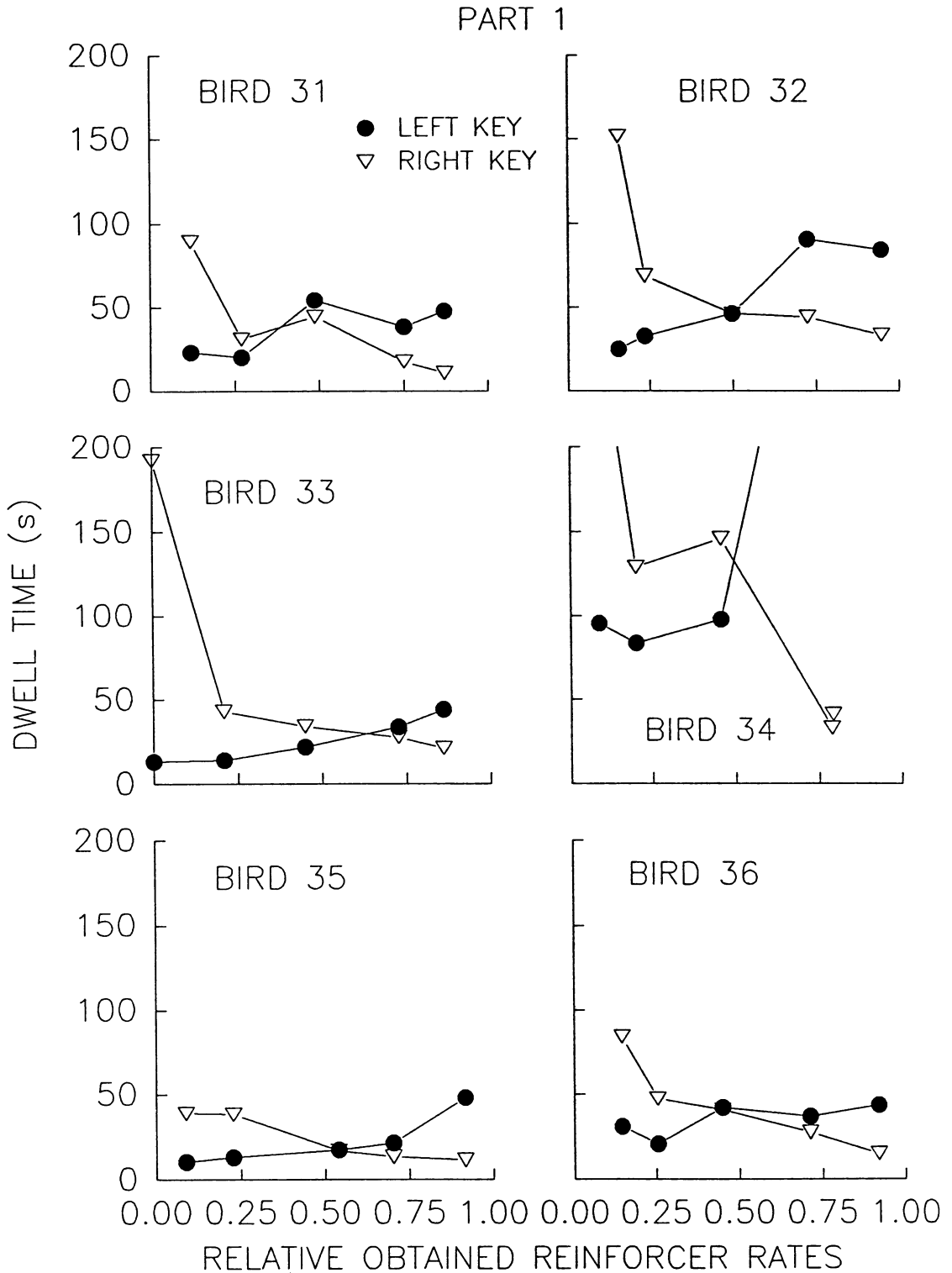


Fig. 2. Experiment 1, Part 1. The mean number of seconds spent responding on each key between changeovers for each bird as a function of the relative left-key obtained reinforcer rate.

PART 2

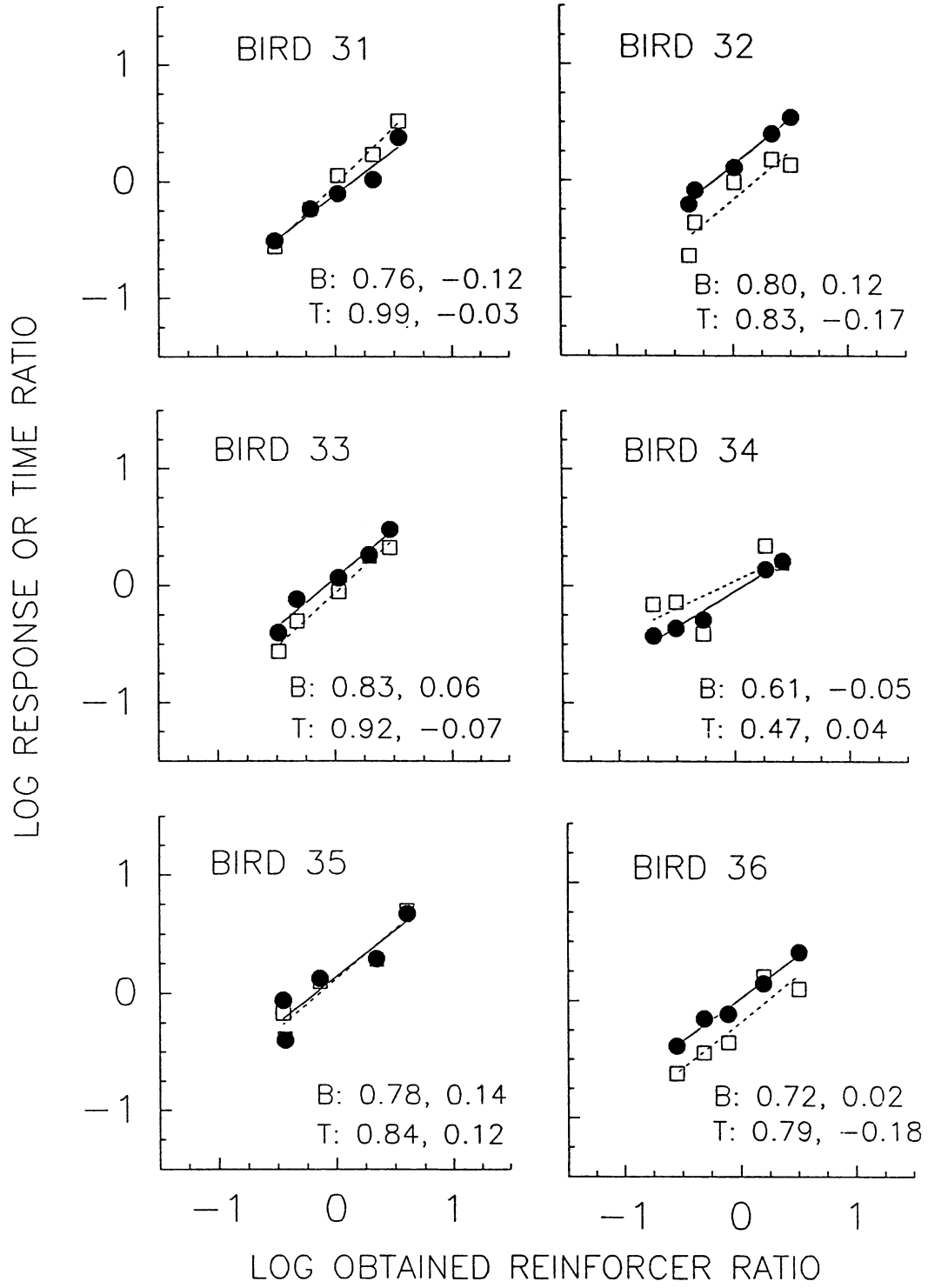


Fig. 3. Experiment 1, Part 2. Log response- and time-allocation ratios (L/R) as a function of log obtained reinforcer ratios for each subject when repletion rates were constant and equal and repletion rates were varied. The straight lines are the lines of best fit by least squares linear regression, and the slope and intercept of these lines for response (B) and time (T) allocation are shown on the graph.

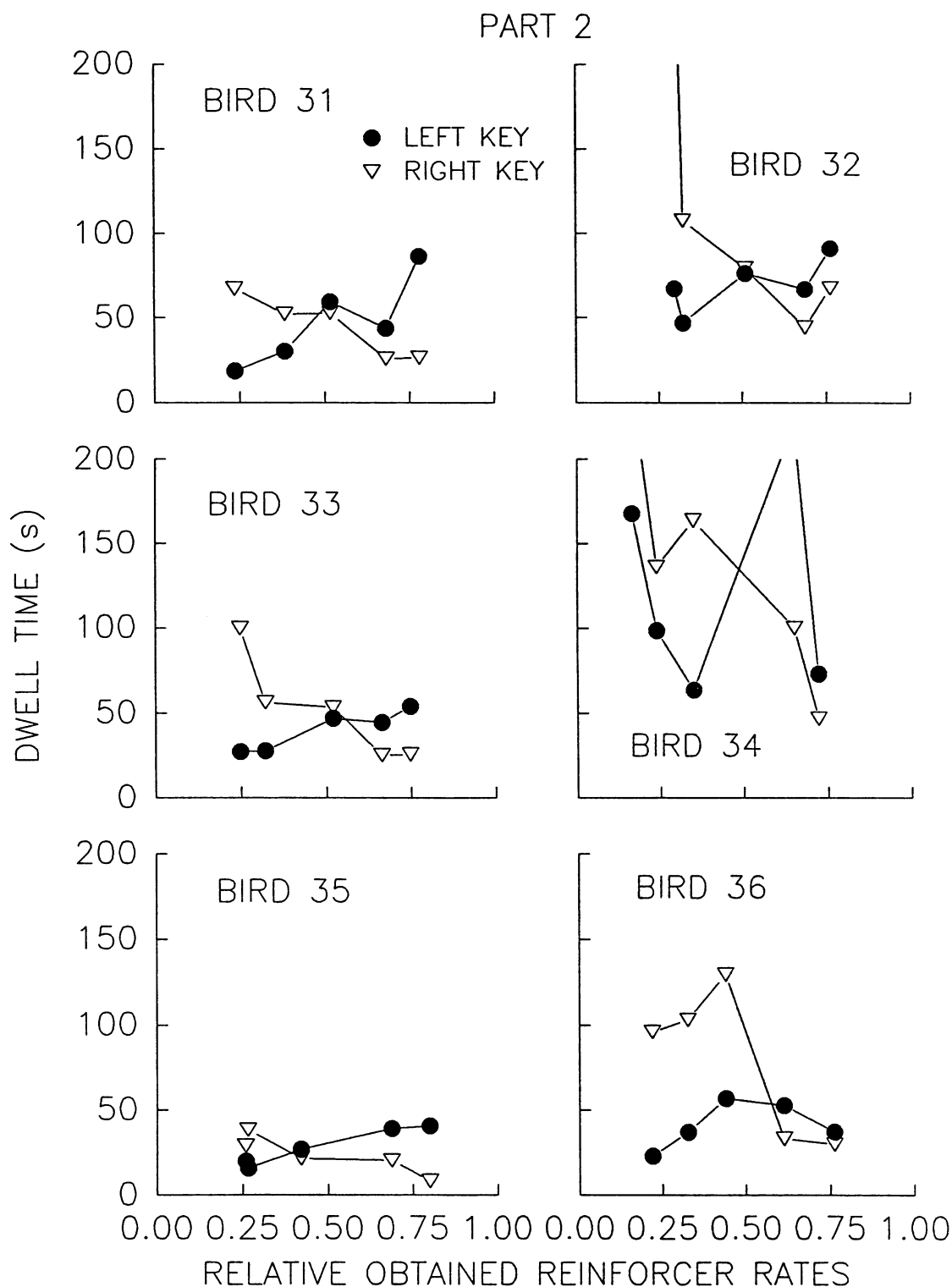


Fig. 4. Experiment 1, Part 2. The mean number of seconds spent responding on each key between changeovers for each bird as a function of the relative obtained left-key relative reinforcer rate. One data point for Bird 32, and two for Bird 34, fell off the graph.

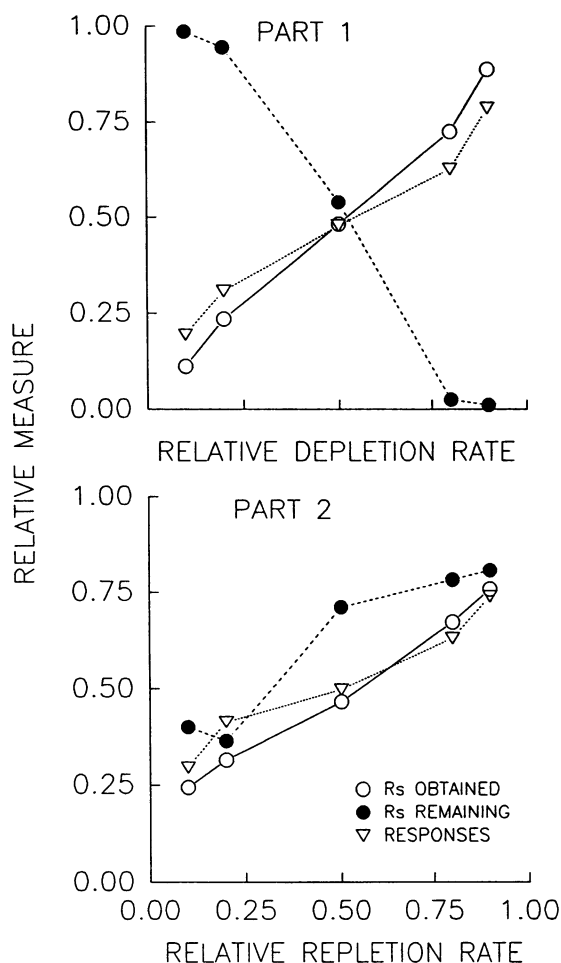


Fig. 5. Experiment 1, Parts 1 and 2. Relative left-key responses emitted, reinforcers obtained, and reinforcers remaining as a function of arranged relative depletion (Part 1) and repletion (Part 2) rates. The data were averaged over the last five sessions for the 6 subjects.

in a very similar way in Parts 1 and 2. However, although very few reinforcers remained on the higher depletion-rate keys in Part 1, generally few reinforcers remained on both keys in Part 2, indicating a reasonably efficient (at a session level) performance.

When few reinforcers (or none) remain at the end of sessions, it is likely that the subjects have spent some time during the session responding on a key at which no reinforcers remain. From the data that were collected in Parts 1 and 2, it is a reasonably simple matter to calculate the percentage of time responding on a key when that key's store had been depleted to zero. These data are shown in Figure

7 as a function of relative depletion or repletion rates. In Part 1, the percentage was surprisingly high on higher depletion-rate keys, was zero, overall, on lower depletion-rate keys, and followed relative depletion rate. The data from Part 2 followed a U-shaped function of relative repletion rate, being lowest when the repletion rates were equal and highest when they were maximally different.

DISCUSSION

The generalized matching relation describes log choice ratios as a linear function of log obtained reinforcer ratios (Figures 1 and 3). The slope of this relation is termed *sensitivity* (Lobb & Davison, 1975), and the intercept to the relation is termed *bias*. The consistent result from Experiment 1 was that distributions of behavior emitted conformed to a generalized matching relation with distributions of obtained reinforcers in both parts, and that the parameters of the relation were not statistically different between the parts. Following the evidence of Vaughan (1981), this relation may not be taken as a theory of choice, but rather only as a descriptive relation. The question that arises from Experiment 1 is whether any of the more usual theories of matching can predict the obtained performances and their empirical similarity as a function of obtained reinforcer ratios in Parts 1 and 2. Two theories were tested. The first, melioration theory (Herrnstein, 1982; Herrnstein & Vaughan, 1980), suggests that animals will dynamically allocate time spent responding between choices so as to move toward an equality in the local rate of reinforcers obtained from each choice. Equality may be attained if not prevented by environmental constraints. A second theory is maximization theory (e.g., Rachlin, Battalio, Kagel, & Green, 1981), in which animals are thought to change their behavior so as to optimize the production of some good. The most obvious good to be optimized in the present experiment would be the overall rate of food reinforcers (see Staddon & Motheral, 1978).

Neither of these theories is easily tested analytically in the present experiment because of the dynamic relation between spending time at one patch, depleting that patch to possibly zero food, and simultaneously increasing the store of food on the other patch. Thus, the theories were tested by simulation. *Stat* subjects responded at once per second on average,

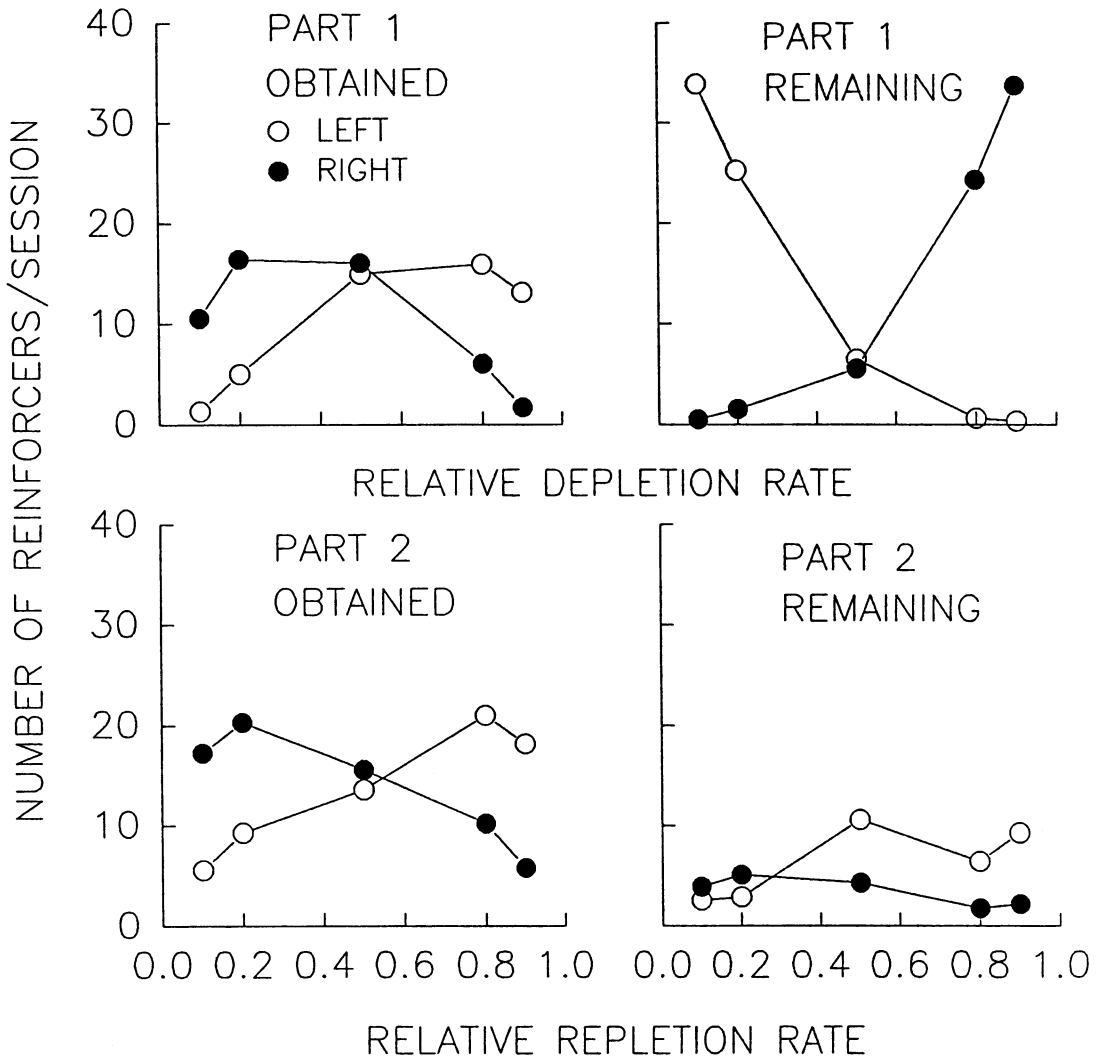


Fig. 6. Experiment 1, Parts 1 and 2. Absolute numbers of reinforcers obtained and remaining after the average session on each key as a function of relative depletion (Part 1) and repletion (Part 2) rates. These data were averaged across the last five sessions for the 6 subjects.

and changed patches with an overall average of once per 40 s, the approximate dwell time with equal schedules (Figures 2 and 4). The probability of changing over per second was constant and was determined for each key by the current interchangeover time for that key within the constraint mentioned above. Responses were produced every 0.33 s with a probability of .33. The *stat* birds responded on the conditions of Parts 1 and 2 with a procedure identical except for one modification: Sessions were 100 reinforcers, not 40, in duration. This was done to provide better estimates of

local or overall reinforcer rates than could be obtained from shorter sessions. At the end of each session, the dwell times on the left and right keys were varied (maintaining a 40-s average) adaptively, the amounts of change decreasing with sessions in a condition. If a variation in preference had produced more equal reinforcer rates (melioration) or higher overall reinforcer rates (maximization) compared with the last session, dwell times were adjusted in that direction by a progressively smaller increment in successive sessions. If not, they were adjusted in the opposing direction.

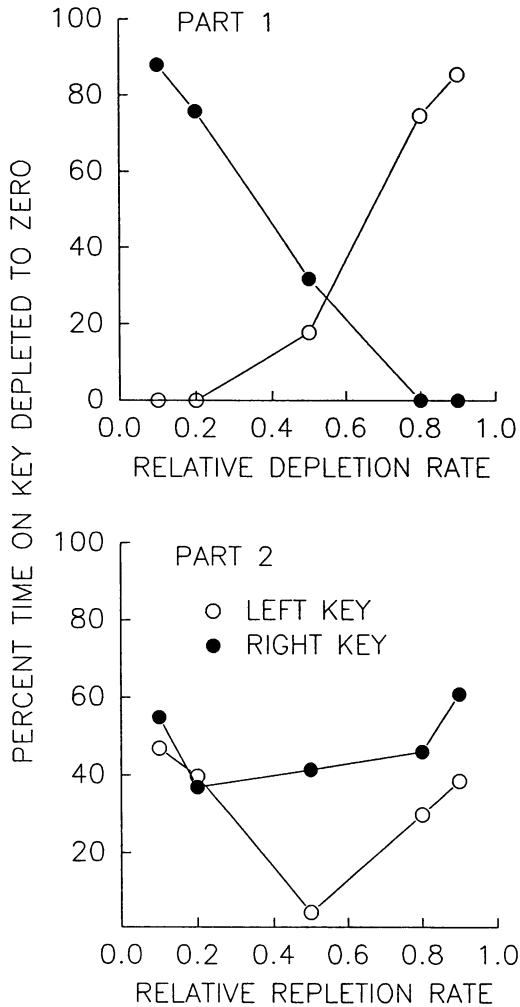


Fig. 7. Experiment 1, Parts 1 and 2. The calculated percentage of time allocated to responding on a key during which reinforcer stores were depleted to zero as a function of relative depletion (Part 1) and repletion (Part 2) rates. These data were averaged across the 6 subjects.

Twenty-five sessions were arranged in each condition, and the last five sessions were used to provide the data shown in Figure 8. In separate sessions, *stat* birds also responded in the same manner as above, but with the probability of changing over fixed at the values obtained for the group data in order to be able to compare theoretically attainable and obtained reinforcer rates.

Figure 8 shows clearly that maximization of overall reinforcer rates did not produce choice functions that were similar to those shown in Figures 1 and 3. The simulations showed that

in some conditions of Part 1, a considerably greater reinforcer rate could have been obtained if a molar maximizing strategy had been used. For instance, in Condition 4, a reinforcer rate three times greater than that obtained could have been produced. In Conditions 3, 5, and 6, approximately twice the rate was attainable. The differences between obtained and attainable reinforcer rates were very much lower in Part 2, and averaged only 1.14 times greater. Melioration theory, on the other hand, produced functions that were very similar in their slopes to the obtained data, although the predicted functions were more S-shaped than were the obtained data. Under the present conditions, melioration theory predicts well. The rather surprising amounts of time spent responding at empty patches in Part 1 (Figure 7) are completely consistent with a melioration model. For instance, when the depletion rate on the left key is much greater than on the right key, the local rate of reinforcement on the left key will also be much greater than that on the right key unless the animal forages the left key to zero and remains foraging there, allocating time but gaining no reinforcers, for considerable periods. These results, then, provide rather unique support for a melioration explanation of choice.

Dwell times on concurrent VI VI schedules have been the subject of some research (Hunter & Davison, 1978; Stubbs, Pliskoff, & Reid, 1977; Tustin & Davison, 1979), and the reported pattern of changes with changing relative reinforcer rate has been similar to that shown in Figures 2 and 4. However, the absolute dwell times on concurrent VI VI schedules are generally much shorter than those found here. For example, Tustin and Davison (1979) reported interchangeover times of 5 to 10 s on concurrent VI 60-s VI 60-s schedules for their 6 subjects. The reason for the longer interchangeover times in the present experiment could simply be due to the fact that the depletion schedules did not time on the patch not currently being worked on. Hence, the probability that a reinforcer would be obtained immediately following a changeover to return to a patch was no greater than when the subject had left that patch, except when that patch had been depleted to zero before the patch was vacated. Two variables may determine when a patch is left: real or apparent depletion to zero of the present patch, and repletion of the

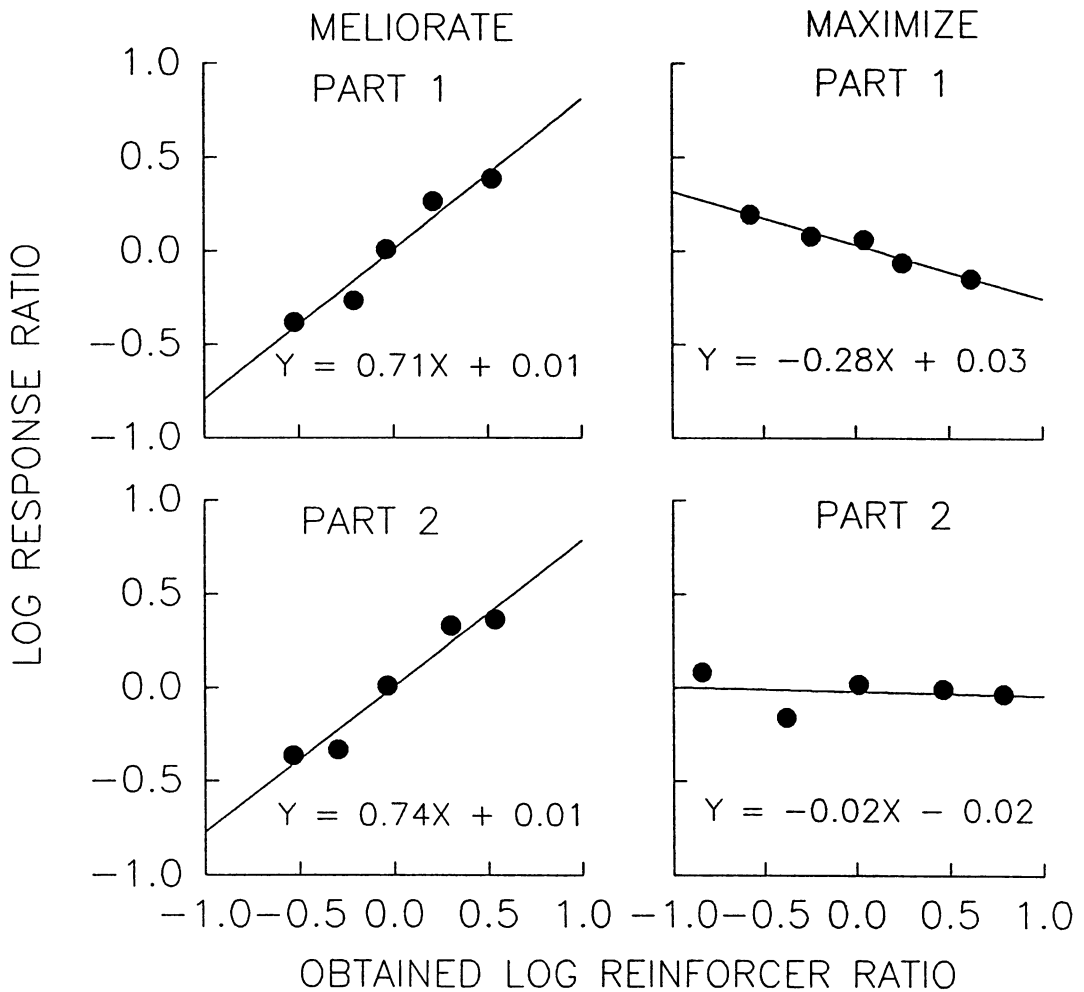


Fig. 8. Data produced by *stat* birds that followed a melioration strategy (left panels) or a molar maximizing strategy (right panels) in Experiment 1, Parts 1 and 2. Log response ratios were plotted as a function of log reinforcer ratios as in Figures 1 and 3. Best fitting straight lines, and their equations, are shown for each strategy and each part of the experiment.

alternative patch. Animals, of course, do not change over between schedules if the alternative schedule does not operate in some way to increase the value (immediacy, magnitude, or some other controlling variable) *relative to the current patch* (see Dreyfus, Dorman, Fetterman, & Stubbs, 1982). For instance, Herrnstein and Loveland (1975) showed that small differences between response requirements on concurrent variable-ratio schedules, which operate only when animals are responding on them, produced exclusive responding to the smaller requirement. In cases like that, however, patches being foraged do not deplete to

zero after a time in the patch. If they did, changing over would most likely occur because the alternate patch would have accrued relatively more value than the current patch. The benefit of the present procedure using separate repletion and depletion schedules is that it allows the control from both the leaving patch and the alternative patch to be separated experimentally. For example, if prey in a patch became easier to catch as a function of time spent on the alternate patch (i.e., a locally richer depletion schedule following a change-over), then, compared with the present procedure, dwell times would likely be shorter.

EXPERIMENT 2

In Experiment 2, Part 3, equal depletion probabilities per second were varied from .0075 to .025, and the repletion probabilities of .0272 and .0068 per second were alternated between the keys. In Part 4, two depletion rates of .04 and .01 reinforcers per second were alternated between the keys, and the equal repletion probabilities were varied from .005 to .03. The sequence of conditions is again shown in Table 1.

RESULTS AND DISCUSSION

The dwell, or interchangeover, times obtained in Part 3 are shown in Figure 9. As would be expected from the results of Part 2, the dwell time on the higher repletion-rate keys was greater in 32 of the 42 cases, which is statistically significant at $p < .05$ ($z = 3.55$). The difference, though, is somewhat obscured by some evident biases between the keys. For instance, the dwell times on the lower repletion-rate key for Bird 34, and on the higher repletion-rate key for Bird 36, were clearly strongly related to which key provided these reinforcer rates. Overall, average dwell times were 72 and 45.1 s when the higher reinforcer rate was on the left key and 44 and 70.8 s when it was on the right key, thus giving approximately the same sensitivity to reinforcement as found in Part 2.

Part 3 dwell times showed no statistically significant trend ($p > .05$, nonparametric trend test, Ferguson, 1971) across increasing depletion rates, although again this lack of trend could have resulted from the effects of bias. A more sensitive method of investigating whether there were any effects of absolute depletion rate is to plot the log ratios of responses emitted, times spent responding, and obtained reinforcers as a function of absolute depletion rate. These are shown separately for the higher and lower repletion-rate keys in Figure 10. None of these measures changed significantly (nonparametric trend test, $p > .05$) with depletion rate. Point estimates of response- and time-allocation sensitivity also showed no significant trends and averaged 0.97 and 0.91, respectively.

The dwell times obtained in Part 4 are shown in Figure 11. Dwell times on the higher depletion-rate alternative (which averaged 61 s) were greater than those on the lower depletion-

rate alternative (average 33.5 s) in 24 of 30 comparisons (significant on a sign test at $p < .05$). There was no significant trend in dwell times on either the higher or lower depletion-rate keys with changes in repletion rate. These results thus replicate the general finding of a preference toward a higher depletion-rate alternative reported in Experiment 1.

Log response, time, and obtained reinforcer ratios in Part 4 are shown in Figure 12. All three measures increased significantly with increasing absolute repletion rate ($p < .05$). However, point estimates of response-measured sensitivity to reinforcement showed no significant trend (averaging 0.69), whereas time-measured sensitivities did increase significantly ($p < .05$) and almost monotonically from 0.31 at a repletion probability of .005 per second to 0.78 at a repletion probability of .03 per second.

Figure 13 shows the calculated percentage of the session time on each key that the subjects in Parts 3 and 4 spent responding at a totally depleted patch. As would be expected, in Part 3, this percentage was zero at low depletion rates, but as depletion rates increased, percentages increased, with the measure on the lower repletion-rate key greater than that on the higher repletion-rate key. The pattern was quite different in Part 4. Time spent at a depleted patch decreased with increasing repletion rate for both patches, and was greater for the higher depletion-rate patch. Although both these general patterns are understandable in terms of the mechanics of the patches, it remains odd, according to some notions of performance, that considerable time was spent responding on depleted patches when reinforcers remained available, albeit at a lower rate, at an alternative patch (e.g., with depletion probability per second between .0125 and .0175 in Part 3, and repletion probability per second greater than .01 in Part 4).

Simulations to obtain the predictions of both the melioration and the maximization models for both Parts 3 and 4 were carried out as in Experiment 1. In general, the melioration model predicted dwell times in the correct direction. But, unlike the obtained data (Figure 9), the melioration model predicted that dwell times on the higher reinforcer-rate key would increase significantly (nonparametric trend test, $p < .05$) with increasing depletion rate in Part

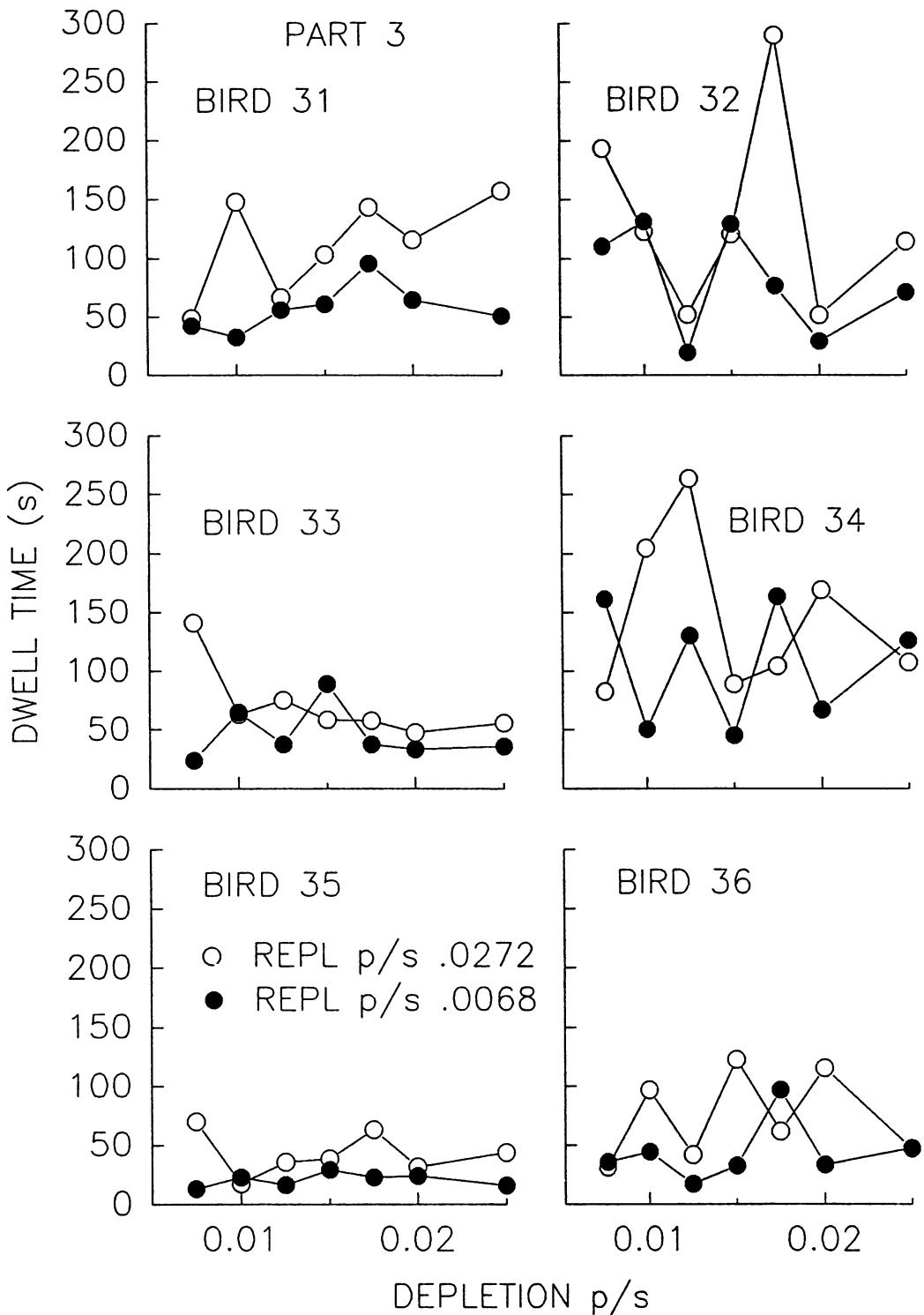


Fig. 9. Experiment 2, Part 3. Dwell, or interchangeover, times for each subject as a function of overall depletion rate. The data are plotted separately for the higher and lower reinforcer-rate alternatives, which were alternated between the keys in successive conditions.

PART 3

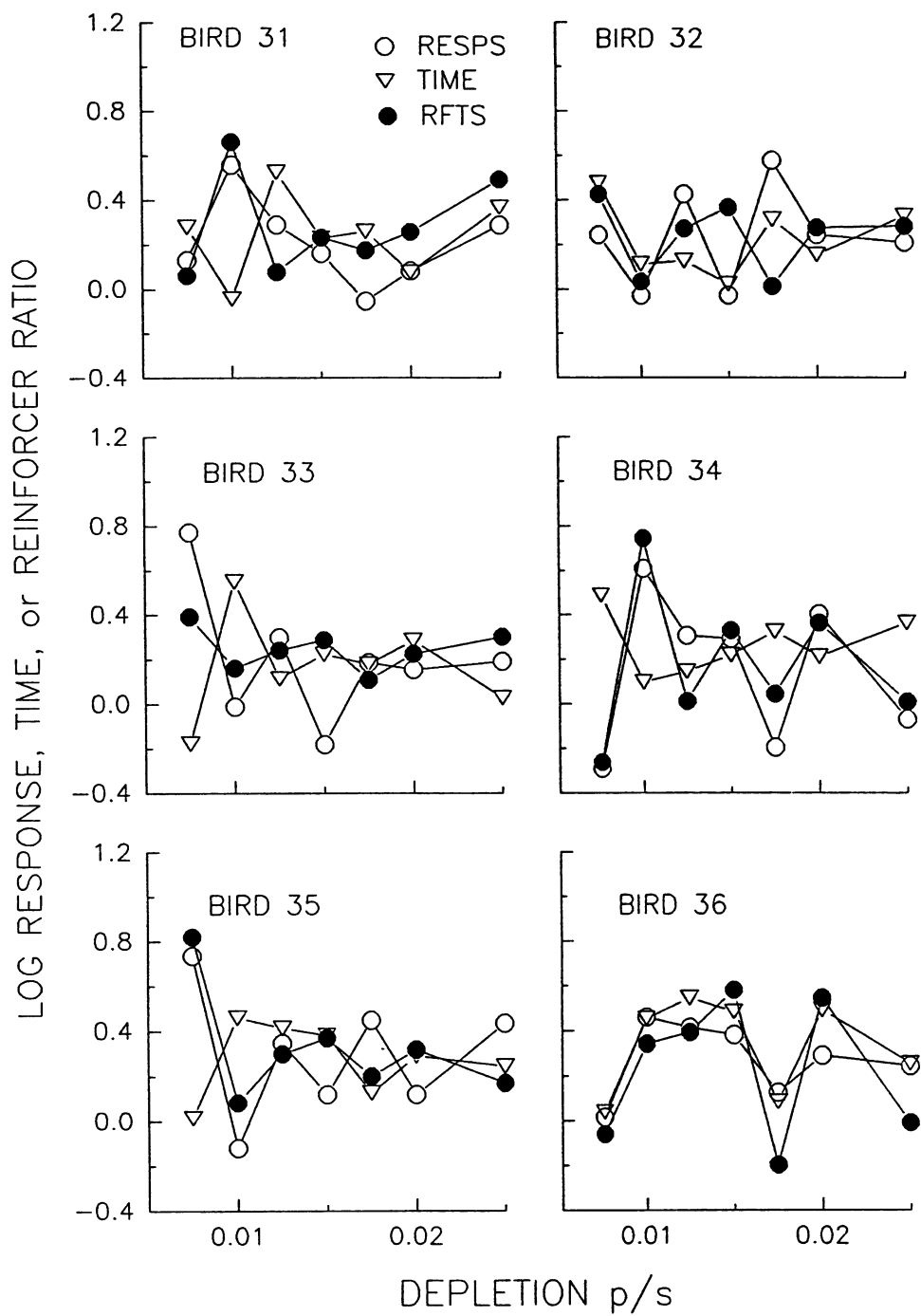


Fig. 10. Experiment 2, Part 3. Log response, time, and reinforcer ratios (higher over lower repletion-rate keys) as a function of overall depletion rate for all subjects.

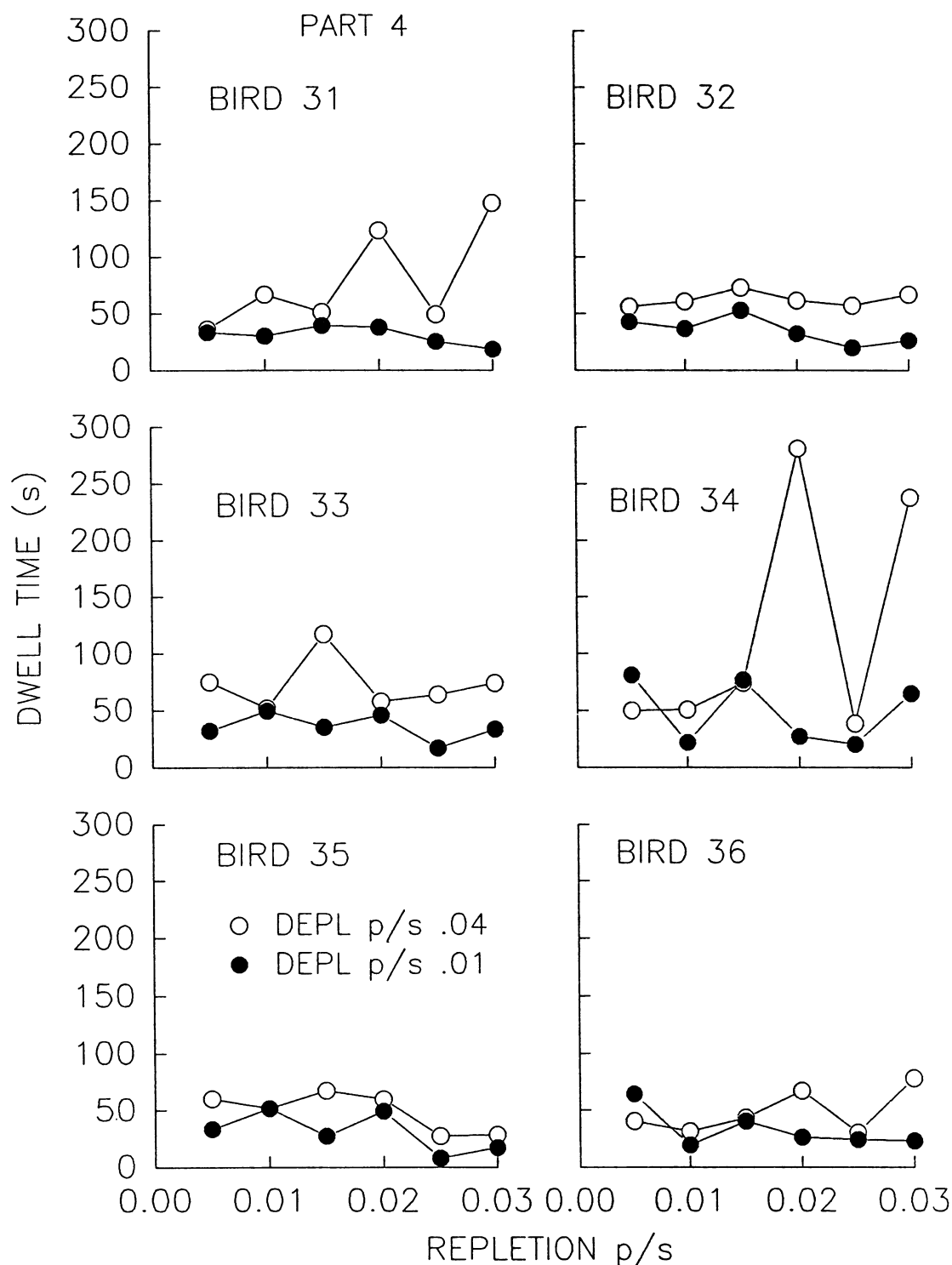


Fig. 11. Experiment 2, Part 4. Dwell, or interchangeover, times for each subject as a function of overall repletion rate. The data are plotted separately for the higher and lower reinforcer-rate alternatives, which were alternated between the keys in successive conditions.

PART 4

LOG RESPONSE, TIME, or REINFORCER RATIO

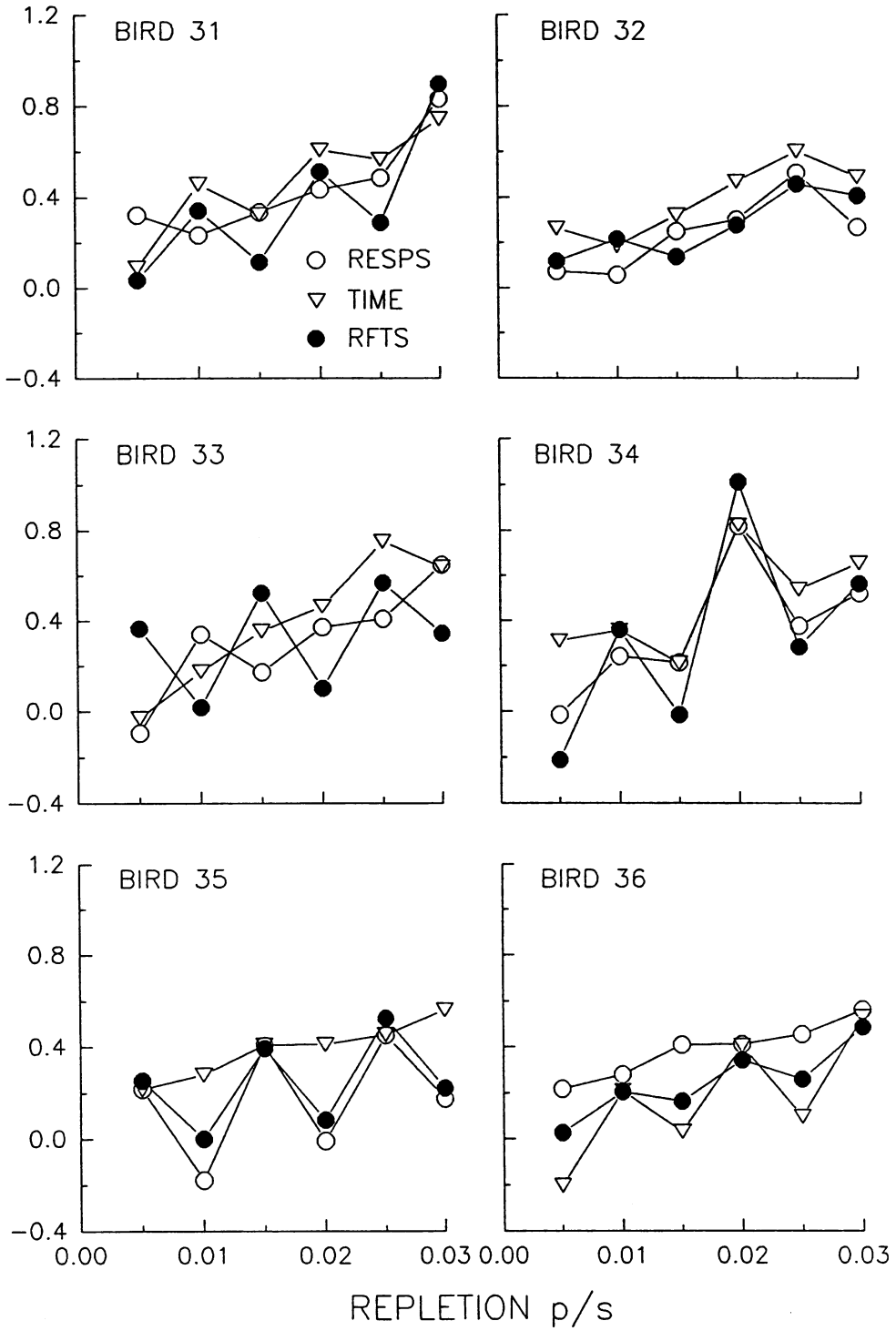


Fig. 12. Experiment 2, Part 4. Log response, time, and reinforcer ratios (higher over lower depletion-rate keys) as a function of overall repletion rate for all subjects.

3. In Part 4, the melioration model predicted that repletion rate would significantly increase dwell time on the higher depletion-rate key and significantly decrease it on the lower depletion-rate key. This was not found (Figure 11). The melioration model thus did not accurately describe the present data.

Molar maximizing simulations accurately predicted no trend in dwell times on either alternative in Parts 3 and 4. In Part 3, this model reasonably accurately predicted a preference toward the higher repletion rate but erroneously predicted a reversal of this preference at low depletion rates (Figure 9). In Part 4, maximization incorrectly predicted a general preference toward the lower depletion-rate alternative.

GENERAL DISCUSSION

The present research investigated pigeons' performance in a modified concurrent-schedule procedure. The modifications that were arranged were designed to provide a somewhat closer approximation to common environmental conditions found in the wild. Rather than arranging, at most, a single food delivery to be available on entry into a patch, multiple food deliveries were often available, with the increment in these stored reinforcers being linearly related to the time just spent away from the patch. Further, patches did not replete when the subjects were working on the patches; this aspect may be more ecologically valid for some foraging species and prey types than for others. Finally, a procedural dissociation was made between the rates at which prey are replenished in a patch (repletion schedules) and the rates at which foraging subjects can obtain these prey in a patch (depletion schedules). It was not a goal of the present research to make the situation more ecologically valid for the pigeon. Rather, one goal was to show how the conventional concurrent-schedule procedure can be generalized so that the effects of the ways in which natural environments behave can be investigated in the laboratory.

The procedures investigated here—manipulating both relative and absolute linear repletion and depletion rates—are, of course, only a very small sample of the procedures that could be investigated. Travel time between patches, nonlinear repletion and depletion, differing maximum carrying capacities between

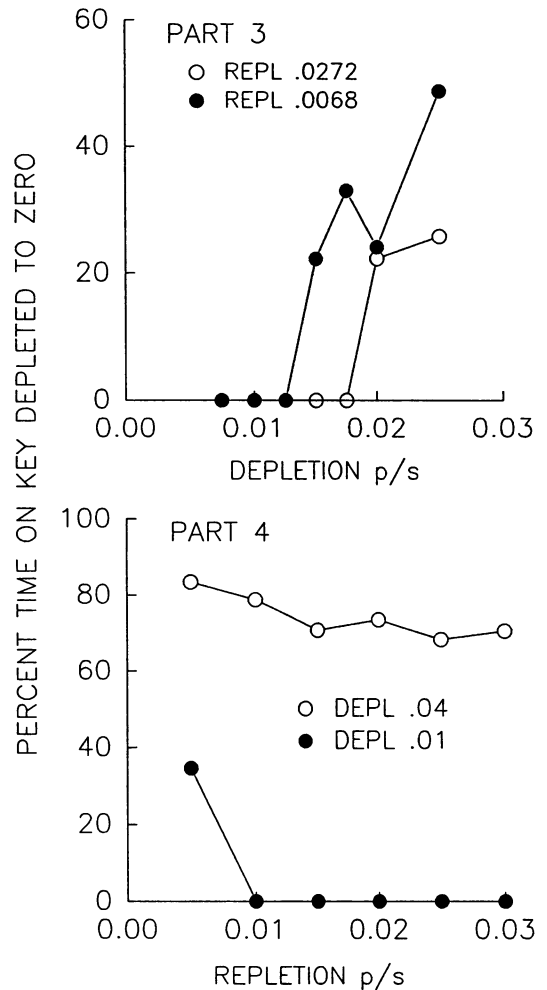


Fig. 13. Experiment 2, Parts 3 and 4. The calculated percentage of time allocated to responding on a key during which reinforcer stores were depleted to zero as a function of overall depletion (Part 3) and repletion (Part 4) rates. These data were averaged across the 6 subjects.

patches, repletion during depletion, and external predation of patches are also prime candidates for experimental analysis.

Given the differences between the present and conventional concurrent-schedule procedures, it was gratifying to find in Experiment 1 that the generalized matching law—the usual quantitative description that applies to concurrent schedules—also described the present results. Subjects showed a linear relation between log response (or time) and log obtained reinforcer frequency ratios (Figures 1 and 3). It did seem that the slopes of these were gen-

erally lower than those usually reported for concurrent VI VI schedules (Baum, 1979; Taylor & Davison, 1983), and the results of Part 4 provided some partial clue as to why this might be. In Part 4, it was found that time-allocation sensitivity increased with increasing absolute repletion rate, indicating that the repletion rates of 0.017 per second used in Part 1 did not produce optimal sensitivity to reinforcement. However, no such change was found in response-measured sensitivity in Part 4, so the apparently low sensitivity in Part 1 remains to be further investigated.

Both absolute and relative time allocation to patches are important measures in the ecological study of foraging. In Parts 1 and 2, time measures changed with relative obtained reinforcers in a manner very similar to that widely reported for concurrent VI VI schedules (Dreyfus et al., 1982; Stubbs et al., 1977; Tustin & Davison, 1979). However, the absolute time spent in a patch appeared to be greater than is usually found on concurrent VI VI schedules providing similar reinforcer rates. Because patch residence stopped the repletion of that patch, shorter dwell times might be expected in the present procedure. However, the longer dwell times may have resulted from substantial stores of reinforcers available in a patch, although such a notion is gainsaid by the considerable times that subjects spent in patch residence when no reinforcers were available (Figures 5 and 13). It appears, then, that the rather long absolute residence times may be a function of some other process.

That other process could be melioration. This theory (Herrnstein, 1982; Herrnstein & Vaughan, 1980; Vaughan, 1981) suggests that animals will dynamically distribute their times spent responding so as to move, within the constraints imposed by the environment, to equalize the *local* rates of obtained reinforcers. Thus, were we to assume by way of example that two stores with differing depletion rates and equal repletion rates were arranged, melioration theory would suggest that more time should be allocated to the higher depletion-rate schedule and less to the lower depletion-rate schedule. If the higher depletion-rate schedule store does not become depleted, this reallocation will not change the local reinforcer rates. However, as soon as the store for the higher depletion-rate schedule becomes depleted, the local rate of reinforcement would

begin to fall until, at some point, this local rate would be equal to the depletion rate on the lower depletion-rate schedule. Over this dynamic change, the local reinforcer rate on the lower depletion-rate schedule will not change because the store associated with this schedule will increase, rather than deplete to zero. The rule of thumb for strict melioration is thus, in the present experiment, to deplete the higher depletion-rate store to zero and then to continue to allocate sufficient time for responding under extinction to equalize the local rates. Under such conditions, considerable numbers of reinforcers should remain at the end of the session on the low depletion-rate alternative (Figure 6).

At a more molar level, although melioration theory provided a reasonable quantitative and conceptual explanation for the response- and time-allocation changes in Parts 1 and 2, it failed to predict quantitatively for Parts 3 and 4. A modification to melioration theory, called *threshold melioration*, has been suggested (Davison, 1990) to provide predictions of the more typical undermatching found in conventional concurrent VI VI performances. As Davison showed, this modified theory predicts that, with a constant threshold, sensitivity will increase with increasing overall reinforcer rates (Alsop & Elliffe, 1988). Because overall reinforcer rates increased significantly (nonparametric trend test, $p < .05$) in both Parts 3 (with increasing depletion rate) and 4 (with increasing repletion rate), increases in sensitivity would be expected in both parts. An increase was found only for time-allocation sensitivity in Part 4. Thus, the threshold melioration theory may also be incomplete.

What are the implications of the present research for foraging in natural environments? First, as shown by Houston (1986) and by Gray (1990), birds distribute the time they spend at two patches according to the generalized matching law even in situations that are distinctly different from the usual laboratory concurrent-schedule procedure. These researchers, along with Baum (1974), reported that groups of subjects followed the generalized matching relation, and Gray was also able to show that the individuals comprising the groups also conformed to the generalized matching relation. The present research generalized these findings to situations in which capture rates and repletion rates were different

(although this would probably also have been the case in the research reported by Houston). But, conformation to the matching relation fails to provide an acceptable theory of patch choice because of the problems associated with the nonconstancy of putative constants in generalized matching. These problems were summarized by Davison (1988), and to these could be added the relation between sensitivity to reinforcement and competitive ability reported by Gray.

Another implication for natural foraging is the finding in Part 3 that absolute depletion rate did not affect response or time allocation, compared with the finding in Part 4 that increasing absolute repletion rate did increase behavior allocation. In Part 4, though, reinforcer ratios also increased, through the mechanical interaction of behavior and the repletion/depletion schedules. The general result of Part 4, then, simply replicates a point on the function describing the results of Part 1, but the reasons for the reinforcer-ratio change require an explanation from an adequate theory. As shown here, such a theory is not currently available. Equally inexplicable, however, is the increase in time-allocation sensitivity with increasing repletion rate in Part 4.

In studies of foraging, it is often found (Fantino & Abarca, 1985; Pyke, Pulliam, & Charnov, 1977) that increases in the profitability of patches increase the selectivity of choice. The same result was shown here in Part 4, in which preference for the higher depletion-rate alternative increased with increasing repletion rate. However, this increased preference was correlated with an increase in the frequency of obtaining reinforcers on the higher depletion-rate alternative. It appears that the change in response allocation can be accounted for entirely by these changes in reinforcer frequencies. But the change in time allocation, which was associated with a sensitivity increase, cannot be fully accounted for. The increasing specialization with increasing abundance documented in previous research has often—perhaps invariably—been associated with increases in *frequencies* in obtaining the preferred reinforcer, and thus these results could be due simply to mechanical changes in the relation between responses and reinforcers changing the reinforcer ratios when abundance is increased. However, the change in

time-allocation sensitivity with repletion rate in Part 4 is a finding that indicates a more fundamental effect of repletion on abundance. The present research, though, suggests that a more careful analysis is required of what prey “abundance” is. In both Parts 3 and 4, overall reinforcer rate increased significantly with increasing depletion and repletion probabilities, respectively, but only in Part 4 was there a significant increase in specialization. “Abundance” consists of two parts: the repletion frequency of the prey, and the depletion frequency, which could be likened to the frequency of obtaining prey during searching. Only increased repletion frequency increased specialization, whereas increases in the frequency of obtaining available prey did not. The distinction between these two variables, and between their effects, must have important implications for both foraging theory and choice generally. For instance, Alsop and Elliffe (1988) showed that choice and sensitivity to reinforcement in a conventional concurrent VI VI schedule increased with overall reinforcer rate. With repletion and depletion rates the same in each patch in their experiment, the present research suggests that the effect they found is more likely a repletion effect.

The procedure used here is a more general procedure than the traditional concurrent-schedule procedure for studying performance, which calls for continuous choices about patch residence to be made. The results of Experiment 1 provided some unique evidence for melioration (or a similar) theory, because subjects continued foraging patches long after they had been depleted (Figures 7 and 13), even though alternative reinforcers were available and taking these would have increased the subjects’ overall reinforcer rate. Melioration theory, however, did not provide a convincing account of the results of Experiment 2; obviously, further research and theoretical development are required for a full understanding of behavior allocation in foraging situations.

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APPENDIX

Numbers of responses emitted, minutes spent responding, reinforcers obtained, changeovers, and reinforcers uncollected. The data are summed over the last five sessions of each experimental condition.

Subject	Condi- tion	Responses		Time (min)		Reinforcers		Change- overs (L → R)	Uncollected reinforcers	
		Left	Right	Left	Right	Left	Right		Left	Right
Bird 31	2	6,073	5,713	109.6	89.9	76	80	121	12	53
	3	6,157	2,970	145.8	66.4	81	27	228	2	133
	4	1,500	6,243	43.7	170.1	9	66	114	189	5
	5	7,644	1,483	173.7	38.5	53	8	217	0	176
	6	2,662	6,960	82.7	128.0	32	87	247	113	14
	7	4,773	4,582	131.9	77.4	102	48	181	28	11
	8	2,157	6,973	46.0	166.5	31	101	149	21	4
	9	6,346	2,649	164.1	49.7	98	28	114	11	13
	10	3,591	6,177	71.9	124.1	61	99	143	2	30
	11	4,052	5,154	105.8	93.9	85	80	107	15	28
	12	5,160	2,669	162.5	52.4	88	34	62	0	34
	13	2,852	3,438	76.2	137.3	28	67	71	35	63
	14	3,431	3,876	126.8	84.7	60	44	53	97	17
	15	2,972	4,293	78.9	134.3	34	79	78	39	61
	16	4,706	2,416	115.4	96.8	50	46	104	122	6
	17	1,009	3,652	39.3	180.1	9	48	73	67	29
	18	3,793	2,808	113.4	98.5	49	44	140	102	15
	19	847	5,754	24.0	189.5	11	61	77	333	0
	20	6,620	2,166	139.6	72.0	92	25	169	18	177
	21	2,158	5,868	50.2	162.7	22	89	79	179	0
	22	6,974	3,230	119.8	92.2	99	47	140	6	56
	23	2,694	4,598	66.5	145.4	22	63	131	63	3
	24	4,666	2,228	110.0	101.7	48	39	182	5	8
Bird 32	2	7,037	6,034	99.7	99.4	84	85	129	15	18
	3	8,246	3,893	142.0	69.3	89	34	94	0	126
	4	2,096	4,469	30.4	184.2	7	38	73	169	0
	5	8,714	1,338	153.4	60.6	72	4	109	0	171
	6	3,874	4,501	66.7	140.2	27	88	122	126	3
	7	8,557	3,433	123.6	81.8	114	52	111	20	4
	8	3,563	5,742	39.2	173.5	31	73	35	8	6
	9	8,692	2,501	121.5	90.1	119	37	80	58	4
	10	4,380	5,309	63.2	145.6	53	111	81	13	10
	11	6,374	4,975	92.9	96.4	84	81	73	16	24
	12	9,509	4,090	126.4	78.3	111	58	66	22	13
	13	3,218	3,832	77.1	134.8	45	85	157	18	47
	14	3,147	1,733	164.7	43.6	35	34	34	55	40
	15	2,655	4,506	105.7	98.8	28	65	49	17	96
	16	4,920	1,465	151.1	56.7	54	29	175	55	40
	17	2,642	2,392	111.8	104.5	37	40	51	9	141
	18	3,520	1,846	135.4	77.1	61	23	42	56	42
	19	2,194	4,089	59.5	151.7	34	105	136	237	7
	20	5,664	1,757	156.2	54.5	100	25	164	4	212
	21	2,377	4,778	73.0	138.6	35	103	135	170	8
	22	4,556	2,557	122.4	89.1	84	40	101	12	66
	23	3,588	4,090	79.6	130.5	43	66	129	27	0
	24	2,727	2,306	120.1	91.3	33	18	128	0	39
Bird 33	2	3,530	5,155	75.9	118.1	75	92	208	40	5
	3	4,889	3,495	115.2	94.2	90	34	205	10	91
	4	460	3,159	13.6	198.6	0	23	62	209	0
	5	5,337	1,975	143.5	69.0	97	16	196	5	128
	6	1,775	5,587	52.5	160.3	21	80	224	147	1
	7	5,850	3,205	132.7	75.2	116	59	179	26	2
	8	1,390	3,529	45.4	166.3	27	82	100	5	3
	9	4,541	1,518	142.8	67.9	109	37	159	29	12
	10	2,643	3,477	66.4	134.1	51	108	143	15	10

APPENDIX (*Continued*)

Subject	Condi- tion	Responses		Time (min)		Reinforcers		Change- overs (L → R)	Uncollected reinforcers	
		Left	Right	Left	Right	Left	Right		Left	Right
Bird 34	11	3,262	2,827	93.2	105.9	80	74	119	33	35
	12	4,507	2,112	107.2	69.1	120	60	115	22	12
	13	2,845	4,044	86.9	123.7	53	89	156	3	56
	14	4,247	2,069	128.0	83.3	59	46	133	78	7
	15	2,870	3,022	127.7	84.3	35	68	86	9	142
	16	4,720	3,542	141.5	71.1	61	35	113	72	28
	17	2,778	3,593	108.0	105.2	31	45	100	25	145
	18	3,895	1,303	181.3	30.7	32	13	77	29	71
	19	1,233	5,476	66.3	146.2	30	130	118	245	5
	20	5,131	2,005	167.1	45.1	79	14	156	0	240
	21	2,170	5,116	92.7	117.3	42	122	121	106	7
	22	3,168	2,134	164.3	49.3	52	23	84	2	139
	23	1,921	4,184	103.6	108.0	50	75	125	5	8
	24	1,559	1,938	147.2	63.5	28	30	118	3	16
	2	1,515	3,065	81.5	121.7	37	44	50	101	53
	3	1,672	859	194.3	16.5	26	7	30	0	197
	4	483	3,788	52.5	154.4	6	62	33	145	7
	5	2,045	1,171	184.9	26.0	38	10	38	0	196
	6	1,633	3,850	82.2	126.8	22	87	59	105	26
	7	3,856	2,365	126.8	81.2	83	32	104	62	27
	8	1,222	3,268	86.8	125.8	12	60	31	16	90
	9	2,533	1,835	147.0	66.7	41	22	40	90	13
	10	1,494	3,442	87.0	120.3	21	67	53	26	82
	11	1,917	3,758	57.3	147.5	41	76	54	126	1
	12	3,510	3,292	96.7	113.6	52	51	54	163	3
	13	2,328	4,498	60.4	152.5	36	83	54	43	20
	14	3,253	2,155	71.2	111.9	42	38	41	169	9
	15	3,463	5,785	69.6	136.5	45	96	92	32	19
	16	3,444	2,647	140.4	69.5	36	35	32	80	38
	17	1,215	4,315	37.9	153.6	11	61	45	63	11
	18	2,266	3,412	71.6	139.9	18	33	52	208	5
	19	960	3,186	44.4	162.5	17	77	41	283	30
	20	4,897	2,060	138.5	72.4	86	25	215	26	159
	21	552	3,627	18.6	192.0	6	40	41	244	0
	22	5,809	3,541	103.7	107.4	78	48	84	11	40
	23	2,756	4,797	64.2	146.8	26	59	174	62	0
	24	3,145	3,261	80.8	131.5	49	24	97	3	3
Bird 35	2	7,191	7,308	96.2	93.5	95	81	331	8	22
	3	8,360	6,198	129.5	80.5	80	34	363	5	96
	4	2,643	12,004	44.6	167.3	5	52	258	156	1
	5	10,638	3,237	171.8	40.9	65	6	214	1	162
	6	3,358	8,350	53.6	157.9	21	71	247	125	0
	7	10,219	5,239	135.7	70.7	112	51	209	11	5
	8	3,057	7,659	60.5	146.6	42	116	230	4	10
	9	6,470	1,382	176.2	35.5	88	22	260	5	22
	10	4,462	5,121	84.8	123.9	41	117	258	4	17
	11	5,843	4,390	116.1	92.5	63	87	260	23	38
	12	7,298	3,155	155.3	57.1	89	60	214	27	15
	13	4,467	7,272	91.2	120.2	51	106	229	1	28
	14	7,165	3,393	155.8	55.7	78	49	148	25	21
	15	4,322	7,150	91.1	120.4	39	91	187	13	52
	16	4,542	3,255	144.9	65.5	52	26	245	45	57
	17	3,964	4,945	122.5	93.2	42	51	325	15	168
	18	5,936	1,933	179.0	33.0	53	8	153	12	74
	19	3,236	4,847	78.6	131.2	31	113	273	220	31
	20	6,609	2,332	160.8	47.9	77	27	354	1	196
	21	5,847	5,751	96.1	116.4	47	121	117	102	1
	22	5,933	2,318	151.2	60.9	72	28	134	3	118

APPENDIX (Continued)

Subject	Condi- tion	Responses		Time (min)		Reinforcers		Change- overs (L → R)	Uncollected reinforcers	
		Left	Right	Left	Right	Left	Right		Left	Right
Bird 36	23	5,091	3,378	106.0	106.3	42	80	123	11	2
	24	5,340	3,229	136.1	76.0	46	28	136	2	16
	2	4,291	5,048	92.8	90.1	81	99	133	18	15
	3	4,459	2,728	120.4	89.4	112	45	196	2	85
	4	637	2,849	56.9	155.7	13	75	111	149	2
	5	3,988	1,215	157.1	54.1	68	6	216	5	178
	6	1,949	5,025	64.4	148.0	27	79	188	142	1
	7	4,725	3,377	124.9	78.2	103	65	142	47	5
	8	1,956	4,769	41.2	172.8	24	85	108	24	4
	9	5,665	2,217	117.8	94.1	90	28	190	86	3
	10	3,479	4,944	55.4	154.6	52	107	90	27	4
	11	1,888	2,456	64.5	146.9	55	70	68	105	3
	12	4,765	2,709	104.0	105.8	83	46	134	109	2
	13	2,022	3,955	46.9	163.6	28	87	85	48	1
	14	3,148	2,350	81.9	129.0	50	41	80	176	6
	15	1,605	3,857	43.8	165.5	26	79	81	43	1
	16	4,641	1,792	149.6	60.5	105	30	215	14	57
	17	1,533	4,396	66.4	145.4	25	71	90	34	40
	18	3,016	2,906	97.8	112.4	34	31	189	157	32
	19	1,663	5,107	48.0	163.5	23	98	126	258	3
	20	4,723	2,608	117.0	93.9	84	48	232	74	130
	21	2,057	4,512	59.6	151.8	30	87	136	146	2
	22	4,414	3,023	109.9	102.2	95	50	152	9	56
	23	3,004	4,815	79.9	129.3	34	67	246	45	0
	24	2,698	2,541	81.4	129.8	48	26	121	4	2